



Effects of biodiversity strengthen over time as ecosystem functioning declines at low and increases at high biodiversity

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Abstract: Human-caused declines in biodiversity have stimulated intensive research on the consequences of biodiversity loss for ecosystem services and policy initiatives to preserve the functioning of ecosystems. Short-term biodiversity experiments have documented positive effects of plant species richness on many ecosystem functions, and longer-term studies indicate, for some ecosystem functions, that biodiversity effects can become stronger over time. Theoretically, a biodiversity effect can strengthen over time by an increasing performance of high-diversity communities, by a decreasing performance of low-diversity communities, or a combination of both processes. Which of these two mechanisms prevail, and whether the increase in the biodiversity effect over time is a general property of many functions remains currently unclear. These questions are an important knowledge gap as a continuing decline in the performance of low-diversity communities would indicate an ecosystem-service debt resulting from delayed effects of species loss on ecosystem functioning. Conversely, an increased performance of high-diversity communities over time would indicate that the benefits of biodiversity are generally underestimated in short-term studies. Analyzing 50 ecosystem variables over 11 years in the world's largest grassland biodiversity experiment, we show that overall plant diversity effects strengthened over time. Strengthening biodiversity effects were independent of the considered compartment (above- or belowground), organizational level (ecosystem variables associated with the abiotic habitat, primary producers, or higher trophic levels such as herbivores and pollinators), and variable type (measurements of pools or rates). We found evidence that biodiversity effects strengthened because of both a progressive decrease in functioning in species-poor and a progressive increase in functioning in species-rich communities. Our findings provide evidence that negative feedback effects at low biodiversity are as important for biodiversity effects as complementarity among species at high biodiversity. Finally, our results indicate that a current loss of species will result in a future impairment of ecosystem functioning, potentially decades beyond the moment of species extinction.

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Effects of biodiversity strengthen over time as ecosystem functioning declines at low and increases at high biodiversity

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Key words: biodiversity ecosystem functioning (BEF); ecosystem processes; grassland; mechanism; plant productivity; plant species richness; temporal effects; trophic interactions.

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INTRODUCTION

Biodiversity is decreasing at an unprecedented rate (Butchart et al. 2010) but is essential for sustaining ecosystem services (Cardinale et al. 2012, Naeem et al. 2012) and human livelihoods (Millennium Ecosystem Assessment 2005). High biodiversity is typically associated with an increased mean and decreased variability of many different ecosystem functions (Balvanera et al. 2006, Allan et al. 2013). In addition, evidence mounts that more species are needed to maintain ecosystem functioning across multiple years, sites, functions, or environmental change scenarios (Isbell et al. 2011). Thus, it becomes increasingly apparent that biodiversity is even more important for ecosystem functioning

than indicated by single-function or short-term studies. Experiments have reported that the effect of biodiversity on some individual ecosystem functions strengthened over time; that is, slopes of regressions of functioning on biodiversity became steeper with time after the establishment of plant biodiversity gradients. Examples include aboveground plant biomass (Cardinale et al. 2007, Marquard et al. 2009, Reich et al. 2012), N pools (Oelmann et al. 2011a), belowground plant biomass (Ravenek et al. 2014), soil organisms (Eisenhauer et al. 2012), and resistance to biological invasions (Roscher et al. 2009a). Such strengthening relationships between biodiversity and ecosystem functioning have been explained by increased complementarity in high-diversity communities

(Cardinale et al. 2007, Fargione et al. 2007, Reich et al. 2012), which also provides a mechanistic explanation for positive effects of biodiversity on ecosystem functioning in general. Complementarity occurs if high-diversity communities can outperform low-diversity communities because of interspecific differences, enabling higher levels of functioning, for example, through acquiring more nutrients, using available light and space more completely, or growing at different times of the year (Loreau and Hector 2001). Complementarity also includes facilitative effects; for example, legumes increase nutrient availability for neighboring plants via fixing atmospheric nitrogen (Fargione et al. 2007).

More recently, studies have indicated that biodiversity effects can also be caused by negative feedback effects at low biodiversity that reduce levels of functioning in these communities via activities of antagonistic soil microorganisms (Maron et al. 2011, Schnitzer et al. 2011). Therefore, positive biodiversity effects may not be driven solely by increased complementarity, but also by the dilution of negative plant species-specific feedback effects in more diverse plant communities (Hendriks et al. 2013). Similar to complementarity effects, such feedback effects might need time to develop (Marquard et al. 2013). For example, temporal changes in plant–soil interactions are known to contribute profoundly to ecosystem functioning during plant community assembly (Kardol et al. 2006). Because of the potentially delayed occurrence of negative feedbacks, they may be overlooked in short-term studies. In the context of agricultural monocultures, such decreasing performance over time has been observed for many crops and underlies the principle of crop rotation (Bullock 1992). First, results restricted to the comparison of plant biomass production of individual species in monocultures, and mixtures did not provide evidence for a particularly strong and consistent deterioration of monocultures over time (Marquard et al. 2013). Yet, experimental studies capable of comprehensively testing this effect over time in natural communities, that is, studying a representative number of ecosystem functions along biodiversity gradients, are still missing. If deteriorating ecosystem functioning with time were common across ecosystem services, the implications would be profound: After human-induced biodiversity loss, for example, due to

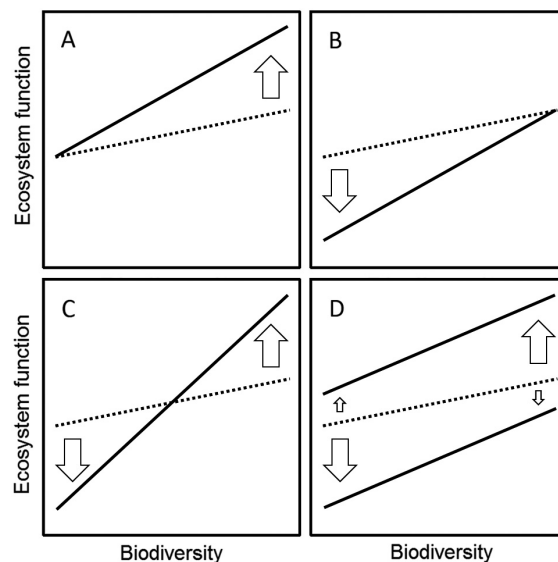


Fig. 1. Schematic illustrating how the slope of the relationship between biodiversity and ecosystem functioning (i.e., the strength of the biodiversity effect) can become stronger over time. Change over time is visualized by arrows. The dotted line visualizes the relationship between the ecosystem function and biodiversity at the onset of the experiment. The biodiversity effect in later years (solid line) can be strengthened by an increasing performance at high biodiversity (A) or a decreasing performance at low biodiversity (B). Both effects are non-mutually exclusive and can occur simultaneously (C). For biodiversity effects to strengthen it is enough if the increase is stronger at high biodiversity, or the decrease is stronger at low biodiversity in the case that the performance at both ends of the biodiversity gradient changes in the same direction (D). In the case of negative biodiversity effects that occur if the measured variable decreases with increasing biodiversity, the logic applies accordingly with inverted signs.

fragmentation or intensified land-use, there would be an ecosystem-service debt that results from the delayed effects of species loss on ecosystem functioning. This ecosystem-service debt would amplify another previously described ecosystem-service debt resulting from delayed extinctions (Isbell et al. 2015).

Conceptually, biodiversity effects can become stronger over time either because of increasing performance at high biodiversity (i.e., the level of functioning achieved; Fig. 1A), decreasing

performance at low biodiversity (Fig. 1B), or a combination of both effects (Fig. 1C). Also when the performance at both ends of the biodiversity gradient changes in the same direction over time, biodiversity effects can strengthen if the increase is stronger at high, or the decrease is stronger at low biodiversity (Fig. 1D). Here, we tested these proposed processes and whether biodiversity effects strengthen over time based on 50 different ecosystem variables indicative of ecosystem functioning (Appendix S2: Tables S1 and S2) that were measured for up to 11 yr in a single large-scale and long-term grassland biodiversity experiment. The Jena Experiment is unique in that a large number of ecosystem variables have been repeatedly investigated over many years in a single experiment. These data enable us to test whether increasing biodiversity effects with time are common and to explore possible drivers for temporal trends. Furthermore, we tested whether temporal changes of biodiversity effects differed among three categories of ecosystem variables: (1) compartment: above- or belowground; (2) organizational level: ecosystem variables associated with the abiotic habitat, primary producers, or higher trophic levels such as herbivores and pollinators; and (3) variable type: measurements of pools or rates. These categories were included in the analysis because a previous study had demonstrated stronger biodiversity effects above- than belowground and for lower compared to higher trophic levels (Scherber et al. 2010), and because rate measures can potentially respond faster to changes in biodiversity than pool measures. As additional covariates, we tested the direction of the biodiversity effect (positive or negative) and the number of times, the first year, and the time span over which the ecosystem variable had been measured.

MATERIALS AND METHODS

Data basis/Jena experiment

At a 10-ha former arable field near Jena (Germany), we established 82 plots, each 20 × 20 m, with a controlled number of plant species, functional groups, and plant functional identity, in a randomized block design (Roscher et al. 2004). Plots were seeded in May 2002 with 1, 2, 4, 8, 16, or 60 perennial grassland plant species, with 16, 16, 16, 14, and 4 replicates, respectively. Plot

compositions were randomly chosen from 60 plant species typical for local *Arrhenatherum* grasslands. Plots were maintained by mowing, weeding, and in early years by occasional applications of herbicide (Roscher et al. 2004). While weeding efforts were higher in plots of lower biodiversity, plots of all biodiversity levels showed large heterogeneity in weeding efforts also within levels (see Appendix S2: Fig. S1).

During 11 yr (2002–2012), a multitude of ecosystem variables have been measured in the Jena Experiment, including measurements conducted above- and belowground, measurements of pools and rates, and measurements on different organizational levels: habitat, primary producers, and higher trophic levels. Measurements on the level of primary producers were conducted on the community of plant species initially sown into the plots to form the diversity gradient, identified as “target plants,” or on plant species that occurred spontaneously in the plots, identified as “weed plants.” In addition, some ecosystem variables have been measured in multiple seasons (spring, summer, autumn, winter), in different soil depths, or with replication. The Jena Experiment is unique in that a large number of ecosystem variables have repeatedly been investigated over many years in a single large-scale grassland biodiversity experiment. Therefore, it offers the possibility to test whether generally biodiversity effects increase with time based on many different ecosystem variables. We based the analysis on 50 ecosystem variables indicative of ecosystem functions (Appendix S2: Table S1) that have been measured in at least 3 years, some much more frequently in continuous time series, since the start of the experiment (Appendix S2: Table S2). Measurements in three different years are the minimum number of repeated measures needed for the statistical approach used in the current analysis. We included ecosystem variables with this low number of repeated measures to keep the number of variables included as large as possible.

Calculating change in biodiversity effects over years

The analysis followed a three-step approach (see Appendix S2: Fig. S2). First, to assess the strength of biodiversity effects, ecosystem variables were regressed individually against the natural logarithm of sown plant species richness,

that is, the variable that was experimentally manipulated in the Jena Experiment. We did so for every year, season, depth level, and replicate individually and included block as a fixed effect fit before species richness. All response variables were Box-Cox-transformed with individually estimated λ for each ecosystem variable per year, season, depth layer, and replicate (boxcox function, MASS package, Ripley et al. 2016; Venables and Ripley 2002) to meet model assumptions of homoscedasticity and normality of errors. Note that this transformation includes the special case of $\lambda = 1$ that signifies that no transformation is applied to the data. Measured proportions were logit-transformed.

The strength of biodiversity effects can be estimated as the slope of the resulting simple linear relationship. Transformation of the response variables caused a curvature in the model predictions. Thus, an average slope was calculated as the difference of performance at high and low biodiversity that were predicted by the model for 60 and 1 species, respectively, and that were back-transformed to the original scale, divided by the length of the biodiversity gradient, that is, $4.09 = \ln(60) - \ln(1)$. This approach is superior to simply averaging measured performance in the monocultures and 60-species plots, respectively, because it is based on the measurements along the whole biodiversity gradient and does not unduly overemphasize potentially diverging measurements at the ends of the gradient. In addition, predicted values from the models and values based directly on the measurements in 1- and 60-species plots were, overall, closely correlated (Appendix S2: Fig. S3).

In the second step, to analyze temporal effects, the slopes of the biodiversity effect were regressed against year for every ecosystem variable, season, depth layer separately, and replicate (Appendix S2: Fig. S2). In the third step, we tested for systematic differences between categories of ecosystem variables (compartment, type, level) and covariates (i.e., the number of times, the first year, and the time span over which the ecosystem variable has been measured and the direction of the biodiversity effect). “First Year” is the year in which the respective variable was measured the first time in the Jena Experiment. For small time spans (i.e., the period of years over which the variable was measured), first year and time span can vary

independently, and both can independently affect observed changes in biodiversity effects because these dynamics might differ in early and later years of the experiment. The direction of diversity effects was included into the model because there could be mechanistic differences how ecosystem variables change in relation to biodiversity over time if these relationships are positive or negative. To test this categories and covariates, we calculated as effect sizes Zr-transformed correlation coefficients from the regressions of slopes of biodiversity effects against time ($Zr = 0.5 \times \ln((1 + r)/(1 - r))$, where r is the Pearson correlation coefficient; Allan et al. 2013, Koricheva et al. 2013). In contrast to correlation coefficients, these effect sizes are suitable for analysis in linear models. Zr-values for ecosystem variables that showed negative relationships between biodiversity and function were multiplied by -1 (indicated in Appendix S2: Table S2), because in the case of a negative biodiversity effect, decreasing slopes over time signify strengthening biodiversity effects. For the few ecosystem variables where switching of the direction of diversity effects occurred over time, the direction of diversity effects that occurred in the majority of the observed years was taken to be the typical direction and to decide about inverting the diversity effect for the analysis. As a result, all resulting Zr-values larger than zero can be interpreted as strengthening biodiversity effects, and values below zero indicate weakening biodiversity effects, independent of the sign of the biodiversity-functioning relationship of the particular ecosystem variable.

All categories were included as explanatory variables into a full mixed-effect model including a random effect for season and a random effect for depth layer nested in the identity of the ecosystem variable ($Zr \sim \text{FirstYear} + \text{TimeSpan} + N + \text{DirectionDivEffect} + \text{Season} + \text{Compartment} + \text{Type} + \text{Level} + (1|\text{EcosystemVariable/Depth}) + (1|\text{Season})$). Categories were tested for significance based on likelihood ratio tests between full and simplified models. All statistics were calculated in R (version 2.15.1; R Development Core Team 2014); mixed-effect models were calculated using the “lmer” function from the “lme4” package (Bates et al. 2014); and prediction intervals from the lmer-models were built with the “sim” function from the “arm” package based on 1000 simulated posterior distributions (Gelman and Su 2014) and are shown in the results as

95% CI. Confidence intervals for the individual ecosystem variables were calculated as effect size (Zr-values) plus/minus 1.96 times the standard error of the effect size, with the standard error being defined as one divided by the square root of the sample size minus three (Koricheva et al. 2013). In the case of multiple measurements of the same variable in different seasons or depth layers, the variance-weighted mean of the effect sizes was calculated. The performance at low and high biodiversity was analyzed in the same way as the strength of biodiversity effects by calculating Zr-values based on correlations of the predicted performance at high and low biodiversity against year. These Zr-values were tested for the importance of the same explanatory variables as the strength of biodiversity effects.

Investigating the processes causing changes in the strength of biodiversity effects over time

To investigate the processes underlying changing biodiversity effects over time, we partitioned the change in the strength of diversity effects over time into the contribution of (1) changes in functioning at low biodiversity and (2) changes in functioning at high biodiversity. These contributions cannot be estimated from the Zr-values used in the analyses described above because close correlations of slopes or performances with time, and thus high Zr-values, can also occur for relationships with shallow slopes given low variation around this slope. Consequently, we based this analysis directly on estimates of the magnitude of change over time. To do so, we converted the change in slope of diversity effects per year into a change in the absolute effect of diversity per year, by multiplying the slope with 4.09, that is, the length of the biodiversity gradient in our experiment: $\ln(60) - \ln(1)$. The resulting change in absolute effect per year (ΔBEF) is in the same units as the change of functioning at low ($\Delta\text{EF}_{\text{low}}$) and high diversity ($\Delta\text{EF}_{\text{high}}$) over time. Consequently, ΔBEF can be partitioned into these two processes ($\Delta\text{BEF} = \Delta\text{EF}_{\text{high}} - \Delta\text{EF}_{\text{low}}$). At any given time, the absolute diversity effect is the performance at high biodiversity minus the performance at low biodiversity; integrating over time the absolute change in biodiversity effects over time is the change in high biodiversity over time minus the change in low biodiversity over time. We then calculated for each ecosystem variable the relative

contribution of changes in functioning at low biodiversity to the overall change of the biodiversity effect by dividing through the absolute biodiversity effect ($\text{Cont.EF}_{\text{low}} = -\Delta\text{EF}_{\text{low}}/\Delta\text{BEF}$) and the corresponding contribution of changes in functioning at high biodiversity ($\text{Cont.EF}_{\text{high}} = \Delta\text{EF}_{\text{high}}/\Delta\text{BEF}$). A sample data set and an illustration of the full analysis together with the required R-code for the analysis are provided in Appendix 3.

Summary statistics

The overall change in the strength of biodiversity effect over time is given by the analysis of Zr-values described above. To illustrate the results for individual ecosystem variables, we also calculated the proportion of ecosystem variables for which significant changes over time in the strength of biodiversity effects and the performance at low and high biodiversity were observed. The number of variables that showed a significant relationship in at least one season or depth layer measured was counted separately for positive and negative effects and divided by the number of investigated variables (50). Note that this headcount approach is conservative because of the low probability to detect significant effects for the individual variables given the often low number of repeated measures. Similar to the Zr-values described above, directions of effects were inverted for variables with negative biodiversity effects so that positive numbers mean “better” for all ecosystem variables.

Sensitivity analysis for length of biodiversity gradient

A sensitivity analysis for the importance of the 60-species plots was conducted, because these plots are replicated only four times in the design of the Jena Experiment, while all other species richness levels were replicated at least 14 times. Therefore, the calculation of biodiversity effects was repeated after excluding all measurements performed on 60-species plots resulting in a biodiversity gradient from one to 16 plant species (levels 1, 2, 4, 8, and 16 species).

RESULTS

Change in biodiversity effects over time

Across all functions, the strength of the biodiversity effect increased with time. This effect was

independent of the compartment, organizational level, and type of ecosystem variable tested despite large variation of the effect among individual ecosystem variables (Fig. 2A, Table 1). This means that the difference between the achieved levels of functioning at low and high biodiversity increased as the experiment progressed (Zr-value for correlation between slope of biodiversity effect and year over all variables measured: mean $0.35 - 0.29 + 0.24$ (95% CI)). The only covariate that affected the magnitude by which biodiversity effects strengthened, albeit only marginally significantly, was the time span over which an ecosystem variable was measured (Fig. 3A, Table 1). This indicates that biodiversity effects continue to become stronger over time also in later years. Summarizing the effects of the individual ecosystem variables investigated, 14 out of 50 (28%) of these showed significant positive effects of time on the strength of biodiversity effects (Fig. 4) while less than a third of this number, 4 (8%), showed significant negative effects of time on the strength of biodiversity effects. Results did not critically depend on the inclusion of the four experimental plots with 60-species mixtures. In fact, biodiversity effects calculated for the gradient of 1–16 species correlated almost perfectly with effects on the gradient of 1–60 species (Appendix S2: Fig. S4).

Processes underlying the change in biodiversity effects over time

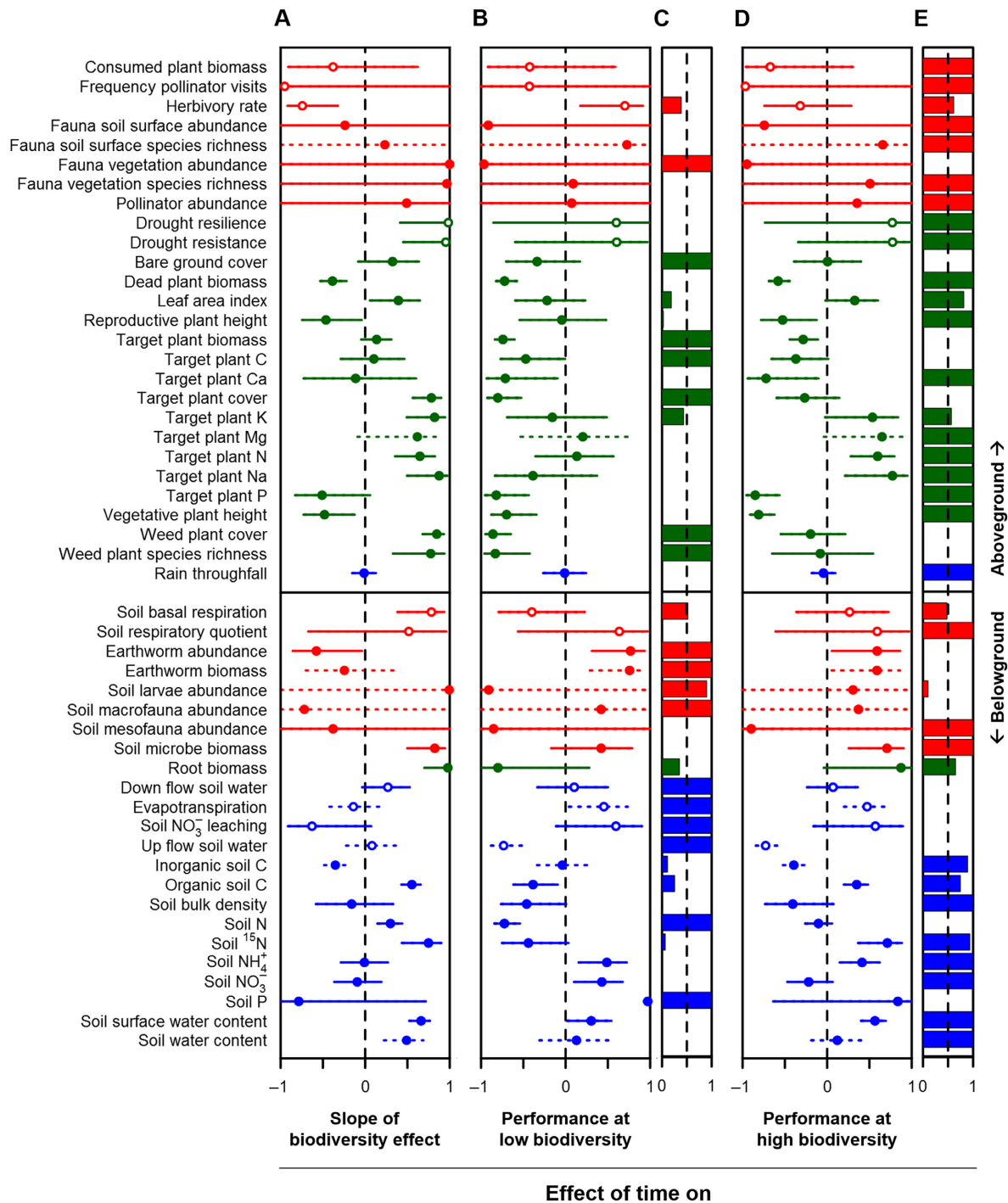
To test whether increasing biodiversity effects over time were caused by decreasing levels of functioning (performance) at low biodiversity, or by improving performance at high biodiversity, we investigated whether performance at high and/or low biodiversity changed over time. Across all investigated variables, the performance of low-diversity communities decreased marginally significantly over time (Fig. 3B, Table 1). This decrease showed significantly higher rates per year for ecosystem variables measured over longer time spans, similarly to effects on the strength of biodiversity effects. We did not observe an influence of any other category or covariate (Fig. 3B, Table 1). The decrease in the performance of low-diversity communities over time was pronounced for some of the investigated ecosystem variables, for example, many measures of plant productivity and soil nutrients (Fig. 2B). Performance at high

biodiversity showed a marginally significant difference between the above- and belowground compartment. Performance at high biodiversity tended to increase for belowground variables over time, while it tended to decrease for aboveground variables (Fig. 2D, Fig. 3C, Table 1). None of the other categories or covariates had significant effects on the change of performance at high biodiversity over time. Summarizing over the individual ecosystem variables, performance at low biodiversity decreased significantly over time for 18% of the considered ecosystem variables, in at least one season or depth layer investigated; performance at high biodiversity increased for 14% (Fig. 4).

Changes in performance at both ends of the plant diversity gradient explain the variation in the observed strength of biodiversity effects (Fig. 2C, E). As hypothesized, both processes contribute to the overall increase in the strength of the biodiversity effect over time. In cases where performance increased at high biodiversity and simultaneously decreased at low biodiversity, the changes at both ends of the plant diversity gradient complemented each other, resulting in a strong overall increase in the strength of biodiversity effects. Examples are leaf area index, soil basal respiration, root biomass, or organic soil carbon. Importantly, there were also cases where the performance at both high and low biodiversity increased over time, yet the biodiversity effect still became stronger over time, because of a higher increase in functioning at high compared to low biodiversity. Examples include drought resilience, drought resistance, target plant N, and soil microbial biomass. The same holds true when the mean level of functioning decreased, but functioning at low biodiversity decreased stronger than that at high biodiversity. Examples for this include target plant cover, weed plant cover, and soil N. Thus, for the biodiversity effect to strengthen over time, it was not necessary that the performance at both ends of the biodiversity gradient changed in opposing directions.

DISCUSSION

Our analysis revealed significant strengthening of biodiversity effects across all the 50 variables investigated. Variables where such effects were most clearly seen included, for example, drought



resistance and resilience, plant cover, soil respiration, root biomass, organic soil carbon, and soil nitrogen. Strengthening biodiversity effects over time are consequently not restricted to particular ecosystem functions, but occurred for a wide

range of different ecosystem functions. While overall only 28% of the investigated ecosystem variables showed significantly strengthening biodiversity effects, we argue that this signal is a strong indication of ecological relevance. We do

Fig. 2. Effect of time on (A) strength (slope) of biodiversity effects, (B) performance at low, and (D) performance at high biodiversity (1 and 60 plant species, respectively) for individual ecosystem variables. Shown are correlation coefficients with 95% CI. Positive values indicate steeper slopes (increased performance) over time. Blue symbols represent functions on the environmental, green symbols on the plant, and red symbols on the consumer level. Closed symbols represent pool and open symbols rate measurements. Dashed error bars depict variables for which no significant biodiversity effect was observed. Confidence intervals that not overlap zero indicate statistically significant changes over time. The two insets with bar graphs (C, E) show the proportion the observed change in the strength of biodiversity effects over time that is explained by changes in the performance at low and high biodiversity. Graphs that show the slopes of diversity effects, performance at low biodiversity, and performance at high biodiversity plotted against time for all ecosystem variables included in the analysis can be found in Appendix S1.

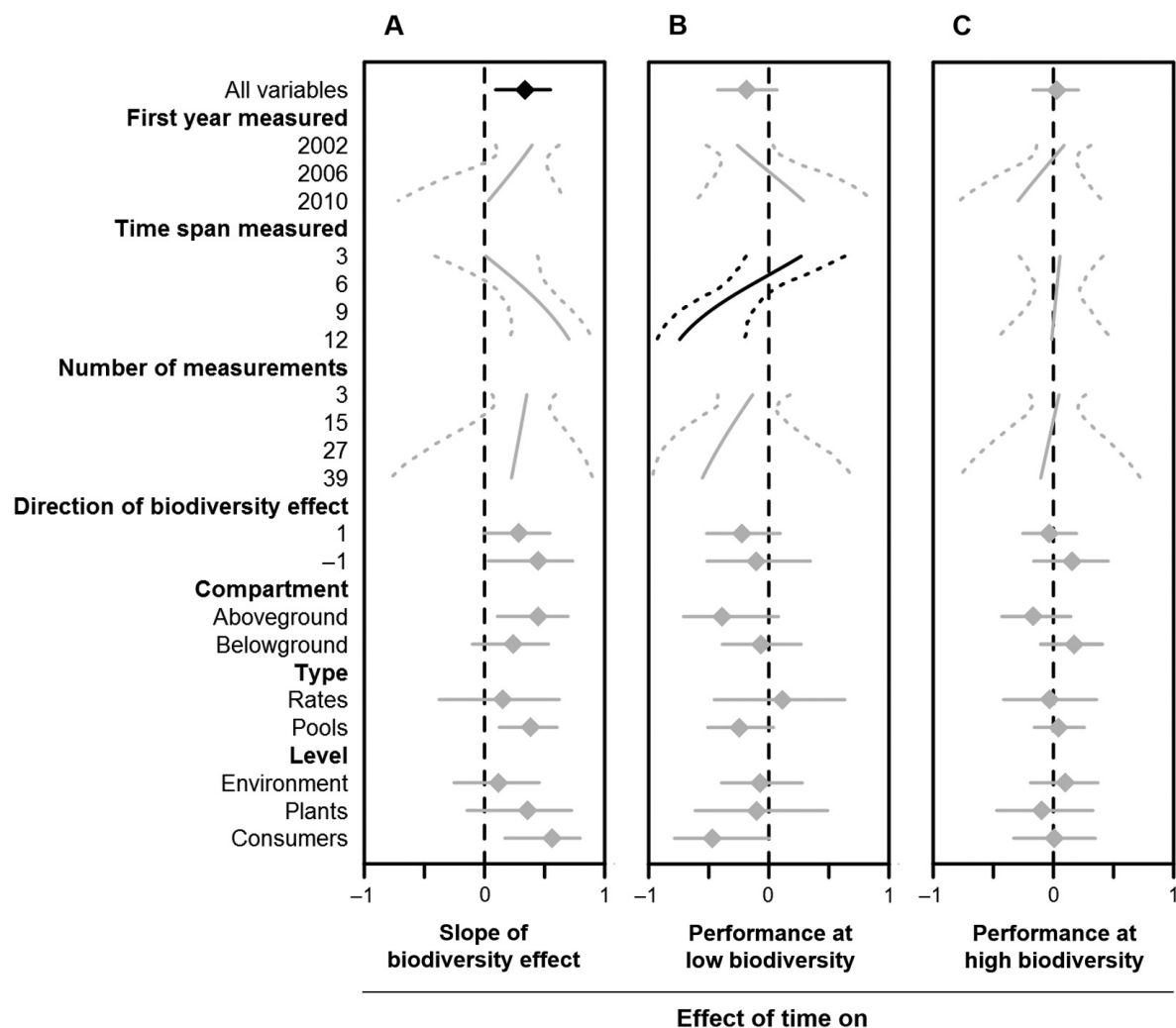


Fig. 3. Summaries for effect of time on (A) strength (slope) of biodiversity effects, (B) performance at low, and (C) performance at high biodiversity (1 and 60 plant species, respectively) for categories of individual ecosystem variables and covariates as described in detail in the text. Categories and covariates for which significant effects were confirmed by a statistical model (Table 1) are shown in black.

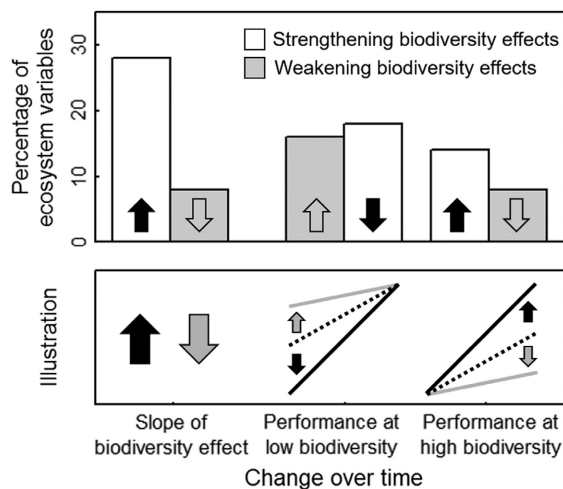


Fig. 4. The percentage of ecosystem variables for which biodiversity effects significantly strengthened (white) or diminished over time (gray) and the percentage of variables for which performance at low and performance at high biodiversity increased or decreased over time. Changes over time are depicted by arrows. These changes in performance contributed to strengthening (white) or to diminishing biodiversity effects (gray) as depicted in the illustration. These are not mutually exclusive, and about 13% of the variables were strengthened both by changes at low and high biodiversity. Note that a decreasing performance at low biodiversity (right bar) causes biodiversity effect to strengthen when performance at high biodiversity stays constant. To calculate proportions, the number of variables that showed a significant relationship (confidence interval of the Zr-value for the regression with year not overlapping with zero) in at least one season or depth layer measured were counted separately for positive and negative effects and divided by the number of investigated variables (50).

so because of the limited temporal replication for many of the variables investigated, and hence the low probability of detecting such effects, and because of the much lower number of variables showing weakening effects. Overall, our results expand the number of functions for which increasingly strong biodiversity effects over time have been documented beyond the previously reported individual ecosystem functions (Cardinale et al. 2007, Eisenhauer et al. 2012, Reich et al. 2012). This increased generality of strengthening biodiversity effects emphasizes the importance of community assembly processes in biodiversity

experiments (Eisenhauer et al. 2012). Thus, one must be cautious to predict consequences of biodiversity loss based on short-term experiments (Isbell et al. 2011, Reich et al. 2012).

Noteworthy, the evidence for deteriorating ecosystem functioning at low biodiversity was stronger in this study than in a previous study that focused on plant productivity alone (Marquard et al. 2013). The documented progressively lower functioning at low biodiversity across various functions is consistent with a build-up of negative plant–soil feedbacks caused by microorganisms (Eisenhauer et al. 2012). However, there are further mechanisms that have been shown to reduce functioning at low biodiversity and thereby could contribute to strengthening biodiversity effects. These include, first, an incomplete use of soil resources combined with leaching losses that cause depletions at low biodiversity and can result in limitations on plant growth and other ecosystem functions (Leimer et al. 2015). While biodiversity effects on NO_3 -leaching decreased over time, effects on soil N showed patterns that are consistent with this mechanism. A second mechanism is recruitment limitations when plant life cycles cannot be completed and the regeneration of new plant individuals is reduced causing a decrease in plant population sizes over time (Symstad and Tilman 2001). In fact, the regeneration of many species in the Jena Experiment has been demonstrated to be seed-limited, with strongest effects in low-diversity communities (Roscher et al. 2009b), and patterns observed for plant cover support this interpretation. A third mechanism is the reduced capacity for temporal turnover between species in low-diversity communities; this turnover is important for maintaining functions such as plant productivity, as different species respond to environmental fluctuations differently (Allan et al. 2011). Consequently, performance at low biodiversity might decline over time because the community lacks members that are adapted to conditions arising from environmental fluctuations or temporal shifts in conditions that occur more often over longer time scales. On the other hand, we can exclude disturbances caused by the maintenance of the field site (i.e., decreased weeding efforts with increasing biodiversity) as alternative explanation for the observed patterns, because of the large heterogeneity in weeding efforts within biodiversity levels (Appendix S2: Fig. S1).

Table 1. Summary of linear mixed-effect models to test the importance of covariates and explanatory categories for the change of (1) the strength of biodiversity effects and performance at (2) low and (3) high biodiversity over time.

Explanatory variable	Response variables		
	Strength of biodiversity effect	Performance at low biodiversity	Performance at high biodiversity
Intercept	$\chi^2_1 = \mathbf{5.03}$; $P = \mathbf{0.025}$	$(\chi^2_1 = 2.82; P = 0.093)^7$	$(\chi^2_1 = 0.08; P = 0.777)^8$
First year	$(\chi^2_1 = 0.34; P = 0.562)^4$	$(\chi^2_1 < 0.01; P = 0.993)^6$	$(\chi^2_1 < 0.01; P = 0.995)^5$
Time span	$(\chi^2_1 = 3.14; P = 0.076)^7$	$\chi^2_1 = \mathbf{5.03}$; $P = \mathbf{0.025}$	$(\chi^2_1 = 0.14; P = 0.712)^3$
Number of measurements	$(\chi^2_1 = 1.30; P = 0.255)^6$	$(\chi^2_1 = 0.36; P = 0.549)^3$	$(\chi^2_1 = 0.01; P = 0.904)^2$
Direction of biodiversity effect	$(\chi^2_1 = 1.05; P = 0.306)^5$	$(\chi^2_1 = 0.05; P = 0.830)^1$	$(\chi^2_1 = 0.60; P = 0.403)^4$
Compartment	$(\chi^2_1 = 0.62; P = 0.432)^1$	$(\chi^2_1 = 0.52; P = 0.471)^5$	$(\chi^2_1 = 3.14; P = 0.076)^7$
Type	$(\chi^2_1 = 0.12; P = 0.731)^3$	$(\chi^2_1 = 0.43; P = 0.511)^4$	$(\chi^2_1 < 0.01; P = 0.949)^1$
Organization level	$(\chi^2_2 = 0.81; P = 0.666)^2$	$(\chi^2_2 = 0.25; P = 0.884)^2$	$(\chi^2_2 = 3.04; P = 0.219)^6$

Notes: The analysis was based on 50 ecosystem variables measured between 2002 and 2012 in the Jena Experiment. Mixed effects were estimated for seasons and different depth layers nested within ecosystem variable to account for the hierarchical error structure. Non-significant explanatory variables (in brackets) have been removed from minimum adequate models in the order of least significance as indicated by superscripts. The covariate season had four levels: spring, summer, autumn, winter; compartment separated functions measured above- or belowground; type differentiated pool vs. rate measures; organization level contrasted ecosystem variables measured on the level of the habitat, the primary producers (plant related), or higher trophic levels. Significant explanatory variables are given in bold.

Ecosystem functioning at high diversity did not consistently increase but tended to differ between ecosystem variables measured above- and belowground. This effect of compartment is consistent with the observation of longer lag phases belowground after the conversion from agricultural land to pasture at the onset of the experiment (Eisenhauer et al. 2012, Ravenek et al. 2014). On the other hand, the marginally decreasing performance of aboveground variables in high-diversity communities over time is likely due to a high nutrient availability shortly after the conversion from an agricultural field to experimental plots, which decreased strongly between the first and the second year of the experiment, and thereafter remained at a stable level for N and further declined for P (Oelmann et al. 2011a, b). Strengthening biodiversity effects via increased performance at high biodiversity can result from complementary effects that become stronger over time. This is especially the case if species increasingly differentiate in their niches during assembly processes. Such selection processes whereby particular “mixture genotypes” are selected have been observed in the Jena Experiment and elsewhere (Zupping-Dingley et al. 2014), resulting in increased functional trait diversity (Roscher et al. 2013). This selection process will take several years. Changes also take place at the species level. For example, grass–legume combinations

are particularly complementary in relation to productivity and N uptake (Hille Ris Lambers et al. 2004, Temperton et al. 2007), but it takes some time for grasses to establish during early succession after sowing when fast-growing legumes have a head start. In addition, an increasingly complete soil community resulting from successional processes in high-diversity communities can increase nutrient mineralization leading to increased plant resource uptake over time (Eisenhauer et al. 2012). Finally, facilitation among plants can strengthen with time, for example, as the rates of symbiotic N₂-fixation by legumes increase (Roscher et al. 2011), with potentially cascading effects on other ecosystem variables due to increased nutrient availability at higher biodiversity (Fargione et al. 2007). The large number of ecosystem variables for which increasing performance at high biodiversity explained the observed increase in biodiversity effects over time confirms the importance of these mechanisms.

CONCLUSION

Analyzing temporal trends in the performance at high and low biodiversity and their contribution to the strength of biodiversity effects have allowed new insights into the processes causing biodiversity to increase ecosystem functioning.

Our results provide evidence across many different ecosystem variables that negative feedback effects in low-diversity communities are as important for biodiversity effects, as complementarity among species in high-diversity communities. Consequently, mechanistic explanations for biodiversity effects should acknowledge that complementary effects are only part of the explanation and that negative feedback effects are significant and important for the low performance of low-diversity communities. Also, our results highlight the importance of long-term experiments because biodiversity effects may be underestimated, as the importance of biodiversity for many ecosystem functions increased with time. Hence, the negative impacts of biodiversity loss are likely greater than suggested by short-term experiments and the full consequences of current loss of species in natural systems might only manifest after years or even decades. Thus, our findings reveal a hitherto largely unnoticed ecosystem-service debt resulting from the current biodiversity crisis that occurs in addition to the service debt resulting from an extinction debt (Isbell et al. 2015) because a loss of species will result in a stronger decrease in ecosystem functioning for several years. Consequently, currently observed adverse effects of biodiversity loss on ecosystem services, as for example the failure of sufficient crop pollination because of the decline in wild bees (Steffan-Dewenter et al. 2005), may only be the tip of the iceberg, as future losses of ecosystem services due to recent biodiversity loss may still be to come. On the positive side, the increase in the functioning of high-diversity communities over time implies that restoring biodiversity will result in increasing benefits in future.

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